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Hierarchical mechanisms of spatially contagious seed dispersal in complex seed-disperser networks

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Abstract. Intra- and interspecific spatially contagious seed dispersal has far-reaching implications for plant recruitment, distribution, and community assemblage. However, logistical and analytical limitations have curtailed our understanding concerning the mechanisms and resulting spatial patterns of contagious seed dispersal in most systems and, especially, in complex seed-disperser networks. We investigated mechanisms of seed aggregation using techniques of spatial point pattern analysis and extensive data sets on mutispecific endozoochorous seed rain generated by five frugivorous mammals in three Mediterranean shrublands over two seasons. Our novel analytical approach revealed three hierarchical and complementary mechanisms of seed aggregation acting at different levels (fecal samples, seeds, pairs of seed species) and spatial scales. First, the three local guilds of frugivores tended to deliver their feces highly aggregated at small and intermediate spatial scales, and the overall pattern of fecal delivery could be described well by a nested double-cluster Thomas process. Second, once the strong observed fecal aggregation was accounted for, the distribution of mammal feces containing seeds was clustered within the pattern of all feces (i.e., with and without seeds), and the density of fecal samples containing seeds was higher than expected around other feces containing seeds in two out of the three studied seed-disperser networks. Finally, at a finer level, mark correlation analyses revealed that for some plant species pairs, the number of dispersed seeds was positively associated either at small or large spatial scales. Despite the relatively invariant patterning of nested double-clustering, some attributes of endozoochorous seed rain (e.g., intensity, scales of aggregation) were variable among study sites due to changes in the ecological context in which seeds and their dispersers interact. Our investigation disentangles for the first time the hierarchy of synergic mechanisms of spatially contagious seed dispersal at a range of spatial scales in complex seed-disperser networks, thus providing a robust and widely applicable framework for future studies.

Key words: associational effects; context-dependence; double cluster; Doñana National Park, Spain; endozoochory; fleshy fruits; invariant proprieties; mammals; mark correlation functions; Mediterranean scrublands; seed-disperser networks; spatial point pattern analysis.

Introduction

Seed dispersal is a critical demographic process that influences plant distributions and the assemblage of entire communities by establishing the first template on which post-dispersal processes such as seed survival, germination, and seedling survival act (Levey et al. 2002, Dennis et al. 2007, Schupp et al. 2010). The spatial patterning of dispersed seeds can range from highly scattered to highly aggregated and it often entails critical plant demographic outcomes (Howe 1989, Schupp et al. 2002). In particular, both intra- and interspecific seed aggregation can influence processes such as the incidence of predators and pathogens (Howe and Miriti 2004, Kwit et al. 2004), secondary dispersal (Forget et al. 2005, Enders and Vander Wall 2012), seedling competition and facilitation (Callaway 2007), as well as chemical and mechanical inhibition (Fenner and Thompson 2005). Consequently, disentangling the proximate mechanisms leading to intra- and interspecific spatially contagious seed dispersal (sensu Schupp et al. 2002) is paramount to comprehend its effects on seed fate, plant recruitment, and the spatial structure of populations and communities.

Precise characterization of intra- and interspecific contagious seed dispersal is, however, a complicated undertaking due to various causes. First, nearly all dispersers disseminate multiple species of plants, and multiple dispersal vectors mediate dispersal of nearly all species of plants (e.g., Carlo et al. 2003, Nathan 2007). Second, disperser species often generate variable levels of seed aggregation, even for a given plant species (Mouissie et al. 2005, Dennis and Westcott 2007, Jordano et al. 2007), and the same disperser can

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potentially generate variable spatial patterns for different plant species (Soons et al. 2004, Clark et al. 2005, Westcott et al. 2005, Fedriani et al. 2010). Third, linking individual disperser species to the disseminated seeds is often technically difficult and thus the contribution of particular animal dispersers to the overall seed rain often remains unknown (Côrtes and Uriarte 2013). The alternative task of quantifying multispecies compound seed rains generated by several dispersers is rarely completed because it is logistically and analytically arduous (but see Carlo et al. 2013). Finally, because seed distribution resulting from such plant–animal interactions is likely to be scale and context dependent (Kollmann 2000, Carlo and Morales 2008, García et al. 2011), finding general patterns often proves challenging (Agrawal et al. 2007). Because of these difficulties, relatively little research has been conducted on spatially contagious seed dispersal, even at the species level (but see Schupp et al. 2002, Russo and Augspurger 2004, Clark et al. 2005), and even fewer have considered complex seed-disperser networks, a range of spatial scales, and several study sites (for a review, see Côrtes and Uriarte 2013). Thus, we clearly need robust analytical frameworks to characterize compound seed rains generated by multiple animal vectors dispersing several plant species at a range of spatial scales and to identify the underlying mechanisms.

Seed dispersal in animal guts (i.e., endozoochory) is a pervasive process that often generates marked multispecific, spatially contagious seed dispersal (Schupp et al. 2002, Kwit et al. 2004, Dennis and Westcott 2007). One overlooked approach allowing the unraveling of mechanisms of endozoochorous seed aggregation is the use of spatial point pattern analysis (Diggle 2003, Illian et al. 2008). This technique deals with the statistical analysis of mapped point patterns (e.g., frugivore regurgitations or feces), which comprise the coordinates as well as additional features of ecological objects (e.g., number and species of regurgitated or defecated seeds within samples). Point pattern analysis can help to identify different proximate mechanisms of seed aggregation and to quantify the overall spatial pattern of the seed rain at a range of spatial scales. Thus, a first level of seed aggregation can be quantified by fitting cluster processes (Wiegand et al. 2007, 2009) to the observed distribution pattern of frugivore regurgitate or fecal samples. However, aggregation of such samples consisting of seeds is not the only potential mechanism of spatially contagious seed dispersal. The use of point pattern analysis within the framework of qualitatively marked patterns (e.g., Wiegand and Moloney 2004, Jacquemyn et al. 2010) facilitates evaluating, for example, whether frugivore feces containing seeds are a random sample of all feces, or if clustered feces are more likely to contain seeds than isolated ones. Finally, a more complete understanding of spatially contagious seed dispersal requires the examination of potential interspecific associations in the number of seeds of particular pairs of species due to, for example, higher than expected frugivore consumption of complementary fruit species (sensu Whelan et al. 1998). This can be achieved by analyses within the framework of quantitatively marked patterns that can detect subtle spatial correlations in the number of different seed species in samples (regurgitates, feces) separated by a given distance (Jacquemyn et al. 2010). Overall, this analytical framework could represent a powerful tool to identify hierarchical structures of seed aggregation as well as their underlying mechanisms.

In this study, we use extensive data on multispecies seed rain to illustrate a novel analytical framework for unravelling patterns and mechanisms of spatially contagious seed dispersal in complex seed-disperser networks. In doing so, we use spatial data and seed composition of fecal samples of five frugivorous mammals that were systematically collected during two consecutive dispersal seasons in three Mediterranean shrublands in southwestern Spain. Specifically, we seek to answer the following three questions that address different potential hierarchical mechanisms of seed aggregation (1) Do frugivores spatially aggregate their feces and, if so, at what spatial scale? (2) Once the spatial aggregation of mammal fecal delivery is accounted for, do frugivore-delivered feces containing seeds aggregate within the overall pattern of all feces (i.e., with and without seeds) and, if so, at what spatial scales? (3) Is there any association among the number of seeds of different pairs of species and, if so, at what scale? Finally, conducting parallel analyses at three different study sites allows us to evaluate the spatial consistency of our findings. Because the relative abundances of seed dispersers as well as the communities of fleshy-fruited plants varied among target shrublands (Perea et al. 2013), we predict spatial variation in the pattern, scale, and strength of seed aggregation for each potential aggregation mechanism.

Methods

Study area and sites

The study was carried out during the dispersal seasons (September–February) of 2005–2006 and 2006–2007 in the Doñana National Park (510 km^2; 37°9′ N, 6°26′ W; elevation 0–80 m above sea level), southwestern Spain. The climate is Mediterranean subhumid, characterized by hot and dry summers (June–September) and mild, wet winters (October–January). The annual precipitation varies widely, ranging between 170 and 1028 mm (583.0 ± 221.1 mm, mean ± SD; $n = 25$ years). The Doñana area is characterized by two main environments: scrubland and marshland. The marshland remains flooded a portion of the year and it is not relevant for this study. The scrubland area, on sandy soils, is made up of patchy, heterogeneous landscapes with a great variety of different habitats.

Because the communities of fleshy-fruited shrubs and relative abundances of dispersers in Doñana largely

differ among habitats (Fedriani and Delibes 2009), we selected three shrublands (separated from each other by at least 7.4 km) within the National Park, as follows. (1) A *Pistacia*-dominated shrubland where the evergreen *Pistacia lentiscus* L., growing alone or in small clumps, is the most frequent shrub. This shrubland also has an understory of *Halimium halimifolium* (L.) Willk, *Ulex* spp., *Cistus* spp., *Olea europaea* var. *sylvestris* (Mill.) Lehr, *Phillyrea angustifolia* L., *Chamaerops humilis* L., and *Myrtus communis* L., together with some scattered trees, mainly *Quercus suber* L. and *Pyrus bourgaeana* Decne. (2) A *Halimium*-dominated shrubland near the marsh border, dominated by *H. halimifolium* and *Ulex* spp., with several fleshy-fruited species including *Rubus ulmifolius* Schott, *C. humilis*, and *P. bourgaeana* trees. *Q. suber* trees are scattered across the area. (3) A *Juniperus*-dominated shrubland located in a dune area dominated by *Juniperus phoenicea* subsp. *turbinata* (Guss.) Nyman and *Juniperus oxycedrus* subsp. *macrocarpa* (Sm.) Ball, with an understory of *Corema album* (L.) D. Don, *Ulex* spp., *R. ulmifolius*, and *H. halimifolium*. *Pinus pinea* L. trees are also common.

Study species

For our analyses, we considered the six fleshy-fruited plant species whose fruits are most frequently consumed by target mammals in the area (Fedriani and Delibes 2009, 2011). Among the one-seeded drupes are *C. humilis* (on average, 1.71 g fresh fruit mass, 669 mg dry seed mass), and *P. lentiscus* (0.10 g, 25 mg dry seed mass). Another drupe (multi-seeded) is *R. ulmifolius* (0.73 g fresh fruit mass, 28.8 seeds per fruit, 2 mg dry seed mass). *C. album* produces berries (0.16 g, 3.0 seeds per fruit, 10 mg dry seed mass). *P. bourgaeana* was the only pome-bearing species (6.75 g fresh fruit mass, 7.9 seeds per fruit, 30 mg dry seed mass). Lastly, among galbuli (juniper fruits), we considered *J. phoenicea* (0.22 g of flesh fruit mass, 7.5 seeds per fruit, 47 mg dry seed mass). The fruit ripening and seed dispersal periods of these species occur from late summer to early winter and thus our extensive sampling encompassed most of the ripening and dispersal seasons of target plants and our detailed data sets allowed for rigorous spatial pattern analyses. Most target plant species rely mainly on mammals for seed dispersal (Fedriani and Delibes 2009), although *R. ulmifolius* and *J. phoenicea* also include birds as important seed dispersers (e.g., Jordano 1984).

Fecal sample collection and seed quantification

We first assessed whether mammals aggregated dispersed seeds simply by clustered fecal marking behavior (e.g., Fragoso et al. 2003). To this end, we collected feces of five mammal species during two consecutive seasons (from September to February, 2005–2007) in the three study sites. The target mammal species were red and fallow deer (*Cervus elaphus* L. and *Dama* L.), wild boar (*Sus scrofa* L.), and two carnivores with generalist feeding habits: European badger (*Meles* L.) and red fox (*Vulpes* L.). These mammals differ in their spatial and fecal marking behaviors. Badgers tend to deliver feces (and within them dispersed seeds) in patterns clearly clustered at small spatial scales, which is consistent with their intensive usage of shared defecation sites (i.e., latrines; Kruuk 1989). Boar feces tend to be lightly clustered, while deer feces are usually spatially scattered (Fedriani et al. 2010). Red foxes often deliver their feces in conspicuous sites (plants, raised spots) and in a relatively scattered fashion (Lloyd 1980). The overall pattern of the multispecies seed rain that emerges from such contrasting disperser behaviors remains uninvestigated for our, and most, study systems.

In each study site, we established a similar-sized plot (72–99 ha) and searched for mammal feces weekly during both years. To ensure that samples were representative of the site, we established between 11 and 13 starting points distributed regularly along the plot edges. During each survey, the observer followed a non-regular zigzag path from a starting point to a non-fixed point on the opposite side of the plot. Then, the observer returned back to the original side following a different path (Fedriani et al. 2010). Each survey (i.e., a transect across the plot and back) took about two hours; overall, about 100 surveys were made in each plot. We collected all feces we found in most (86.8%, $n = 183$) positive surveys, i.e., those where at least one fecal sample was found. In a small fraction of them (13.2%), we collected all carnivore feces (which are locally scarce) and up to the first five deer and boar fecal samples (which are more abundant; Fedriani et al. 2010). Up to 20 pellets per deer fecal group were collected, because each one contains an average of 19 pellets (Tottewitz et al. 1996). A global position system reading was used to determine the coordinates of the mammal feces; these GPS coordinates were then imported into a geographic information system (using ArcView 3.2 software; ESRI 1995). Overall sample sizes were 319, 323, and 253 in the *Pistacia*-, the *Halimium*-, and the *Juniperus*-dominated shrublands, respectively.

Samples were individually stored and air-dried in paper bags at room temperature. Each sample was washed carefully using a sieve (mesh size 0.5 mm) under running water. All seeds and parts of them (e.g., skin, pulp, pedicels) were separated and identified using 20–40× magnifying glasses and a reference sample. The number of intact seeds was recorded and used as a mark in some analyses. Overall, we recovered 205 335 undamaged seeds in geo-referenced feces. Numbers of seeds found, by plant species, were: 182 469 *R. ulmifolius*, 20 578 *C. album*, 1629 *P. bourgaeana*, 252 *P. lentiscus*, 242 *J. phoenicea*/*J. oxycedrus*, and 165 *C. humilis* seeds.

Point pattern analysis

We used different techniques of spatial point pattern analysis (Stoyan and Stoyan 1994, Diggle 2003, Illian et

al. 2008) to investigate three nonexclusive mechanisms of contagious seed dispersal at the levels of the feces samples, seeds, and seed species, separately in each target shrubland (see *Introduction*). In addition to their spatial location, the feces were characterized by "marks" (e.g., species and number of seeds), which were used in the analyses at the seed and seed species levels. To test the fit of data with specific point process models, we conducted simulations of the point processes and estimated simulation envelopes, which are the fifth lowest and highest values of the summary statistics of the simulated process. Observed values above the top or below the bottom simulation envelopes indicate higher or lower than expected aggregation, respectively. Observed values within the simulation envelopes indicate a level of aggregation compatible with the stochasticity of the point process model.

Aggregation of mammal feces at a range of spatial scales

In this case, we used the pair correlation function $g(r)$, the distribution function of the nearest neighbor distances $D(r)$, and the spherical contact distribution $H_s(r)$ to quantify the spatial pattern of feces of target frugivorous mammals (Wiegand et al. 2013*a*). The empirical pair correlation function was used to fit Thomas cluster processes (Wiegand et al. 2007, 2009) to the spatial pattern of feces, and the other two summary statistics were used for testing the fit of these point processes.

The pair correlation function $g(r)$ describes the density of feces at distance r away from "typical" feces, divided by the overall density, λ, of feces in the target study plot. Thus, the $g(r)$ has the intuitive interpretation of a normalized neighborhood density (Wiegand and Moloney 2004). Because of this property, the pair correlation function is well suited to describe spatial clustering, which is indicated by $g(r) > 1$. However, the pair correlation function is usually not sufficient to characterize more complex spatial patterns and must be supplemented with summary statistics that capture different types of spatial information (Wiegand et al. 2013*a*). We therefore used as additional summary statistics the nearest neighbor distribution function $D(r)$, which gives the proportion of mammal feces that have at least one neighbor within distance r, and the spherical contact distribution $H_s(r)$, which gives the proportion of "test locations" that have at least one neighbor within distance r (Illian et al. 2008, Wiegand et al. 2013*a*). Note that the $D(r)$ characterizes the clustering in more detail, whereas $H_s(r)$ characterizes the size of gaps in the pattern (i.e., size of spots without feces). These summary statistics were estimated as described in Wiegand et al. (2013*a*). We used a bin of 3 m and a ring width of 6 m for the $g(r)$ and evaluated the summary statistics up to a maximal distance of 150 m (note that the study areas comprise 72.0–98.6 ha).

To characterize the key properties of spatial clustering of the distribution pattern of mammal feces at our three study sites, we used cluster process as "benchmark" processes with known structure and directly interpretable parameters. To this end, we used the Thomas process (Thomas 1949, Stoyan and Stoyan 1994, Seidler and Plotkin 2006, Wiegand et al. 2007, Wiegand et al. 2009), which is based on a simple stochastic construction principle; it consists of a number of randomly and independently distributed "clusters." The Thomas process describes two basic properties of these clusters: its intensity is given by a parameter ρ (i.e., $A\rho$ is the number of clusters where A is the area of the study site), and its size is given by parameter σ. The Thomas process uses the following rules to distribute feces inside the clusters. First, the feces are randomly assigned to the clusters, i.e., the number of feces per cluster follows a Poisson distribution with mean $\mu = \lambda/\rho$, where λ is the overall density of the pattern of feces. Second, the distribution of the locations of feces belonging to a given cluster, relative to the center of the cluster, is assumed to be a two-dimensional normal distribution with variance σ^2. The cluster size r_C can therefore be defined as $r_C \approx 2\sigma$ and includes ~87% of the feces belonging to a given cluster; the approximate area covered by one cluster is $A_C = \pi {r_C}^2 = 4\pi\sigma^2$. The pair correlation function expected under the Thomas process can be calculated and yields:

$$g(r, \sigma, \rho) = 1 + \frac{1}{\rho}\frac{\exp(-r^2/4\sigma^2)}{4\pi\sigma^2}. \quad (1)$$

This allows fitting of the observed pair correlation function with that of the Thomas process.

The Thomas process describes only one critical scale of clustering (given by the parameter σ). However, in diverse guilds of seed dispersers (as in the present study), it is likely that species-specific spatial and fecal marking behaviors lead to contrasting levels and spatial scales of seed clustering (e.g., Fedriani et al. 2010). To address this possibility, we used the Wiegand et al. (2007, 2009) extension of the simple Thomas process (previously described) to a cluster process where small clusters are nested within large clusters. To this end, a simple Thomas process is generated following the same rules as before, but the points are then replaced by small clusters where the feces are again assigned randomly to the small clusters. This process has four parameters: σ_1 and σ_2 describe the sizes of the large and small clusters, respectively, and ρ_1 and ρ_2 describe the density of the large and small clusters, respectively. The pair correlation function expected under the nested double-cluster Thomas process can be calculated and yields:

$$g(r, \sigma_1, \rho_1, \sigma_2, \rho_2) = 1 + \frac{1}{\rho_2}\frac{\exp(-r^2/4\sigma_2^2)}{4\pi\sigma_2^2} + \frac{1}{\rho_1}\frac{\exp(-r^2/4\sigma_{\text{sum}}^2)}{4\pi\sigma_{\text{sum}}^2}$$

with

$$\sigma_{\text{sum}}^2 = \sigma_1^2 + \sigma_2^2. \quad (2)$$

The unknown parameters of the Thomas processes in Eqs. 1 and 2 were determined using minimum-contrast methods based on the pair correlation function (Stoyan and Stoyan 1994, Wiegand et al. 2007, 2009).

To test the fit of the data with these two point process models, we conducted 199 simulations of the fitted point processes and estimated simulation envelopes, which are the fifth lowest and highest values of the summary statistics of the simulated point process, for the $g(r)$, $D(r)$, and $H_s(r)$. To test the overall fit of the point process models, we also used a goodness-of-fit (GoF) test that collapses the scale-dependent information contained in the test statistics into a single test statistic, u_i, which represents the total squared deviation between the observed pattern and the theoretical result across the scales of interest. The u_i were calculated for the observed data ($i = 0$) and for the data created by the $i = 1, \ldots, 199$ simulations of the null model and the rank of u_0 among all u_i was determined. If the rank of u_0 is larger than 190, there is a significant departure from the null model with $\alpha = 0.05$ over the scales of interest (e.g., 1–150 m). Details about the GoF test can be found in Loosmore and Ford (2006), and Grabarnik et al. (2011).

Aggregation of feces containing seeds within the overall pattern of feces

To find out if mammal feces containing seeds were a random sample of all feces, and to characterize potential departures from this, we used techniques of qualitatively marked patterns and the random labeling null model to represent absence of spatial structure (Wiegand and Moloney 2004). The random labeling null model randomly shuffles the mark "with seed" over all mammal feces (i.e., with and without seeds). To test departures from random labeling, we again used simulation envelopes and the GoF test as described previously.

To quantify the spatial patterns of seeds (of any species) within that of feces, we used mark connection functions (Illian et al. 2008, Jacquemyn et al. 2010, Raventós et al. 2010) as summary statistics. The qualitative mark is of type 1 if the feces contains seeds, and of type 2 if not. A mark connection function $p_{ij}(r)$ gives the conditional probability that, from two feces that are separated by distance r, the first is type i and the second type j (i.e., $i = 1$ or 2; Illian et al. 2008). Mark connection functions are closely related to pair correlation functions:

$$p_{ij}(r) = p_i p_j \frac{g_{ij}(r)}{g_{i+j,i+j}(r)} \quad (3)$$

where the $g_{ij}(r)$ are partial (or bivariate) pair correlation functions that quantify the relative density of type j feces around type i points (Wiegand and Moloney 2004), the $g_{i+j,i+j}(r)$ is the pair correlation function of the unmarked pattern (i.e., feces with and without seeds), and p_i is the proportion of type i feces among all feces. If mammal feces with seeds are a random sample of all feces, we expect $p_{ij}(r) = p_i p_j$ [because in this case $g_{i+j,i+j}(r) = g_{ij}(r)$]. If feces with seeds are aggregated within all feces, we find $p_{11}(r) > p_1 p_1$, and if feces with and without seeds are spatially segregated, we find $p_{12}(r) < p_1 p_2$.

To test if feces containing seeds are preferably located in areas of overall high density of feces (e.g., latrines; Kruuk 1989), we used the test statistic $g_{1,1+2}(r) - g_{2,1+2}(r)$ (Jacquemyn et al. 2010). This test statistic compares the density of feces (i.e., $1 + 2$) around feces with seeds (i.e., type 1) with the density of feces (i.e., $1 + 2$) around feces without seeds (i.e., type 2). The expected value of this test statistic is zero under random labeling, but if feces containing seeds would occur preferably in clusters of feces (latrines), we expect $g_{1,1+2} > g_{2,1+2}$.

Association in the number of seeds of particular plant species

To quantify potential spatial interspecific associations in the number of seeds of the main plant species found in mammal feces, we used the bivariate mark correlation function as a summary statistic (Illian et al. 2008, Getzin et al. 2011, Raventós et al. 2011). The feces had two quantitative marks: the number of seeds of the first species (m_1) and the number of seeds of the second species (m_2). The bivariate mark correlation function $k_{m_1 m_2}(r)$ yields the mean mark product $m_1 m_2$ of two feces separated by distance r (m_1 is taken from the focal feces and m_2 from the feces at distance r), divided by the nonspatial expectation $\mu_1\ \mu_2$, where μ_1 and μ_2 are the mean number of seeds (per feces) of species 1 and 2, respectively. To test if the observed mark correlation function indicates nonrandom spatial correlations in the number of seeds, we contrasted it to a null model that shuffled the mark pairs (m_1, m_2) attached to the given feces together over all feces (Wiegand et al. 2013*b*). To test departures from the null model, we again used simulation envelopes and the GoF test as described previously.

Results

Aggregation of mammal feces at a range of spatial scales

Feces in the *Pistacia*-dominated shrubland were strongly clustered (Fig. 1A). For example, the neighborhood density at distance 7 m was 22 times higher than expected by a random pattern, but this strong aggregation declined rapidly to a density two times the expected density at distances of 20 m (Fig. 1B). Because of the very strong small-scale clustering, the Thomas processes could not completely describe the pattern, but we could fit a double-cluster process (Eq. 2) over the distance interval 5–150 m (rank = 188, $P = 0.065$). Testing the fit with the distribution function of the nearest neighbor distances $D(r)$ shows that the double-cluster process could not describe essential aspects of the observed pattern: the double-cluster process predicted that substantially more mammal feces than observed had their nearest neighbor within distances of 9–50 m (inset Fig. 1B). This means that many feces were isolated

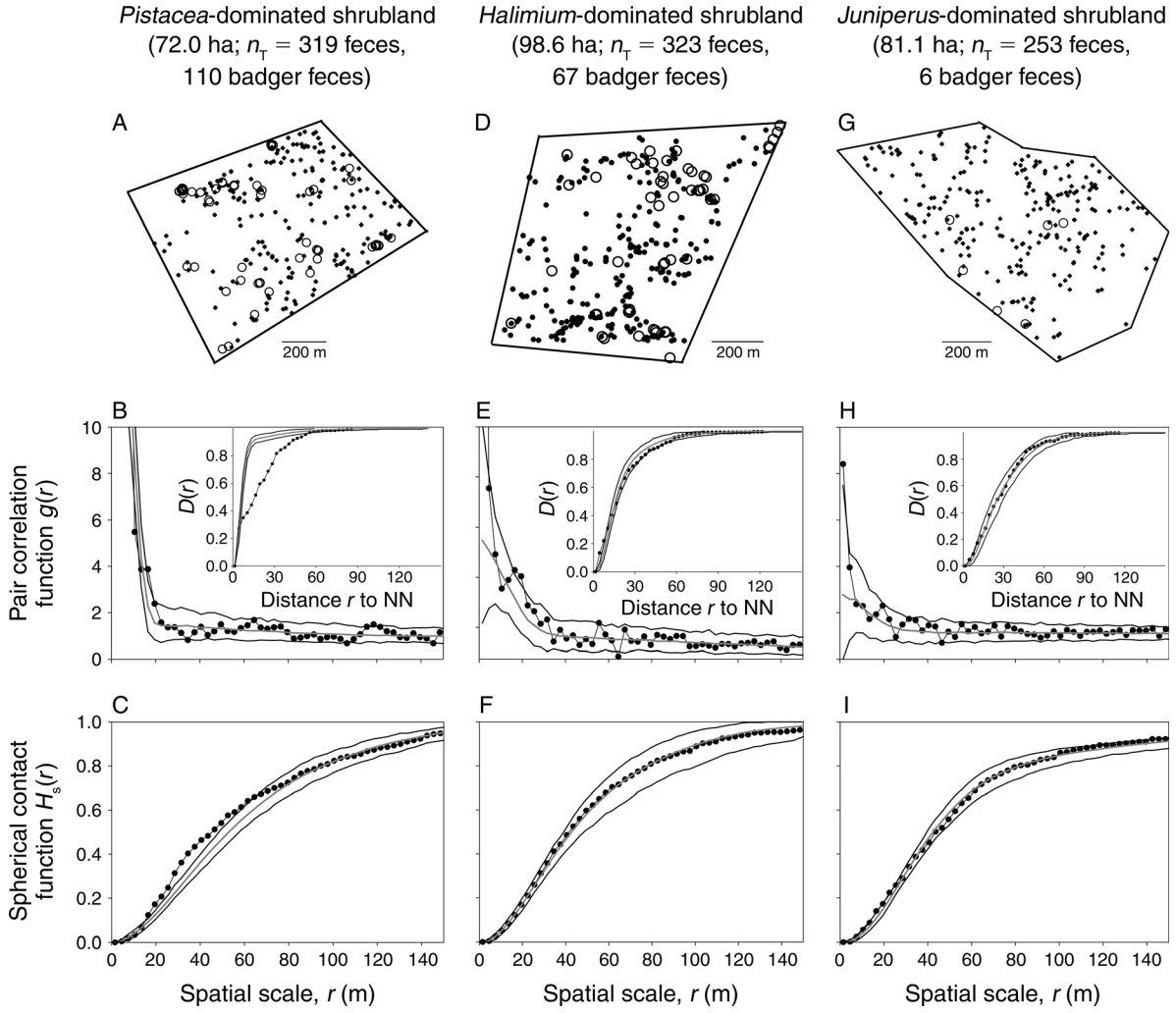

FIG. 1. (A, D, G) Spatial distribution of mammal feces in each of the three studied shrublands; study area size, total number of feces (n_T), and number of badger feces are given. (B, E, H) Point pattern analysis of the pattern of mammal feces using a double-cluster process in each study site, showing the pair correlation function of the data (dots and thin black line), the expected pair correlation function of the double-cluster process (thick gray solid line), and the corresponding simulation envelopes (thick black lines; the 5th lowest and highest values of the pair correlation functions created by 199 simulations of the null model). The small insets show the corresponding test of the fitted process with the nearest-neighbor distribution function $D(r)$, which gives the proportion of mammal feces that have at least one neighbor within distance r. (C, F, I) Graphs are the same as the small insets in panels (B, E, H), but for the spherical contact distribution $H_s(r)$, which gives the proportion of mammal feces ("test locations") that have at least one neighbor within distance r.

(i.e., had their nearest neighbor at larger distances than predicted). Finally, the spherical contact distribution of the fitted point process agreed much better with the observed one (Fig. 1C), but showed some smaller departures at distance range 17–60 m. This indicates that the double-cluster process reproduces the gap structure (i.e., areas without mammal feces) reasonably well, but that some gaps were too large (i.e., caused by the isolated feces).

Because the lack of fit seemed to be related to a few clusters composed of many badger fecal samples with extreme aggregation at a small scale (i.e., latrines), we repeated the analysis without considering badger feces. The spatial distribution of the subset of the fecal sample ($n = 209$) was satisfactorily fitted by a double-cluster process, especially for scales above 2 m (pair correlation functions; rank = 135, $P = 0.330$; Fig. 2A). Testing the fit with the nearest neighbor distances $D(r)$ (inset Fig. 2A; rank = 197, $P = 0.020$) and spherical contact distribution $H_s(r)$ (Fig. 2B; rank = 189, $P = 0.060$) shows that the double-cluster process provides a good approximation of the observed pattern of feces, excluding those of badgers.

Feces in the *Halimium*-dominated shrubland were characterized by a strong aggregation at small scales (1–10 m) and a less marked clustering at larger scales (11–

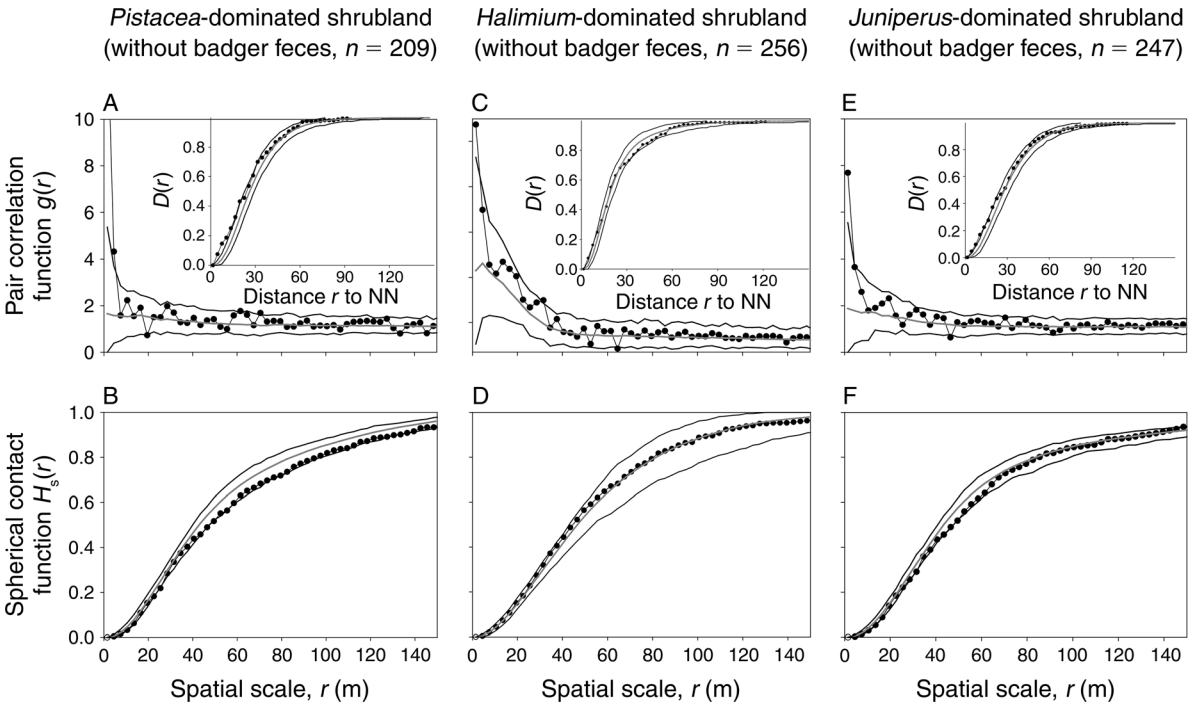

FIG. 2. Point pattern analysis of the pattern of mammal feces, excluding badger samples, in each studied shrubland, using a double-cluster process in each study site. Other conventions are as in Fig. 1.

150 m) (Fig. 1D, E). For example, the neighborhood density at distance 7 m was five times higher than expected by a random pattern. The double-cluster process provided a reasonable description of the fecal sample distribution (rank = 193, $P = 0.040$; Fig. 1D). This was confirmed by the distribution function of the distances to the nearest neighbor (inset Fig. 1E; rank = 196, $P = 0.025$) and the spherical contact distribution (Fig. 1F; rank = 37, $P = 0.820$). Nonetheless, the observed clustering at the small scales was stronger than that predicted by the double-cluster process. As in the *Pistacia*-dominated shrubland, this could be related to the presence of several badger latrines in the area. Indeed, the goodness of fit of the pair correlation function for a sample subset ($n = 256$) without badger feces improved considerably (rank = 160, $P = 0.205$; Fig. 2C), and both the $D(r)$ and the $H_s(r)$ were within the simulation envelopes of the fitted point process model (Fig. 2C, D). This suggests that the strong clustering of badger feces caused the departure from the model, but otherwise the double-cluster process provided a good approximation of the spatial pattern of feces.

The feces in the *Juniperus*-dominated shrubland were characterized by a significant aggregation at small scales (1–15 m) that was less marked at larger scales (16–150 m; Fig. 1G). For example, the neighborhood density at distance 7 m was two times higher than expected by a random pattern. Again, the double-cluster process provided a reasonable description of the observed fecal sample distribution (pair correlation function; rank = 189, $P = 0.060$), especially for scales larger than 2 m (rank = 130, $P = 0.355$; Fig. 1C). The $D(r)$ and the $H_s(r)$ were within the simulation envelopes of the fitted point process model (rank = 181, $P = 0.100$ [Fig. 1H] and rank = 109, $P = 0.460$ [Fig 1I], respectively). Because only a few badger feces were found in this area ($n = 6$), their exclusion yielded only a slightly improved fit of the pair correlation function (rank = 185, $P = 0.080$; Fig. 2C).

Examining the parameters of the fitted cluster processes across study sites (Table 1) allows further evaluation of the spatial consistence of the patterns we have reported. In doing so, we used parameters calculated when badger fecal samples were excluded from analyses, because they provided a better fit. In the *Pistacia*-dominated shrubland, the critical scales of fecal clustering were $r_{C1} = 129.5$ m and $r_{C2} = 18.0$ m for large and small clusters, respectively. The larger clusters contained, on average, 7.3 mammal feces (and 15.4 small clusters); the small clusters contained, on average, 0.5 feces (Table 1). In the *Halimium*-dominated shrubland, the critical scales of fecal clustering were $r_{C1} = 100.7$ m and $r_{C2} = 11.7$ m; the larger clusters contained, on average, 11.3 feces (and 9.1 small clusters), and the small clusters contained, on average, 1.3 feces (Table 1). In the *Juniperus*-dominated shrubland, the critical scales of clustering were $r_{C1} = 184.5$ m and $r_{C2} = 15.4$ m; the larger clusters contained, on average, 9.1 mammal feces (and 20 small clusters), and the small clusters contained, on average, 0.5 feces (Table 1). Thus, even though there were quantitative variations in the level of fecal

TABLE 1. Summary of fit results for the fecal sample distribution data of mammals (excluding badger) using the double-cluster process in three target Mediterranean shrublands in Spain.

Shrubland type and cluster size	N	$A\rho$	σ_{sum}	2σ (m)	μ	ρ_2/ρ_1	σ_1/σ_2
Pistacia-dominated shrubland	209						
Large clusters		28.2	130.7	129.5	7.4	15.4	7.3
Small clusters		433.4		18.0	0.5		
Halimium-dominated shrubland	256						
Large clusters		22.6	101.4	100.7	11.3	9.1	8.7
Small clusters		205.31		11.7	1.3		
Juniperus-dominated shrubland	247						
Large clusters		27.1	185.1	184.5	9.1	20.0	12.0
Small clusters		540.9		15.4	0.5		

Notes: Clusters refer exclusively to feces (not seeds); $A\rho$ is the number of clusters where A is the area of the study site and N is the number of fecal samples. Cluster size is indicated by subscripts 1 (large scale) or 2 (small scale); ρ_1 and σ_{sum} are the fittest parameters of large clusters; ρ_2 and σ_2 are the fittest parameters of small clusters; μ_1 and μ_2 are the average number of feces in one large-scale and one small-scale cluster, respectively; ρ_2/ρ_1 is the average number of small clusters in one large cluster and σ_1/σ_2 is the size of large clusters relative to the size of small clusters.

aggregation, mammal feces were clearly aggregated in the three shrublands and the pattern (double cluster) was relatively consistent across the three target seed-disperser networks.

Aggregation of feces containing seeds within the overall pattern of feces

Once the aggregated distribution of fecal samples was accounted for, analysis of how feces with seeds were distributed within the overall pattern of feces showed that feces with seeds were strongly spatially aggregated at a spatial scale of up to ~50 m for the *Pistacia*-dominated shrubland (Fig. 3A) and the *Halimium*-dominated shrubland (Fig. 3D). For example, for the *Pistacia*-dominated shrubland, the probability that two feces separated by a distance of 20 m have both seeds ($P = 0.450$) was threefold higher than under the expectation of random labeling ($P = 0.15$; Fig. 3A). In the *Juniperus*-dominated shrubland, however, there was only marginal evidence of such aggregation (Fig. 3G). Interestingly, although in the *Pistacia*- and *Halimium*-dominated shrublands, feces with seeds were strongly aggregated, the bivariate $p_{12}(r)$ showed only small departures from random labeling (Fig. 3B, E). Finally, the test statistic $g_{1,1+2}(r) - g_{2,1+2}(r)$ showed that the aggregation of feces with seeds was related to the clusters of feces in both the *Pistacia*- and the *Halimium*-dominated shrublands; feces with seeds had higher neighborhood density of feces (with and without seeds) than expected by random labeling for distances up to 30 m. Thus, the likelihood that single feces contained seeds was larger in clusters of feces as compared with relatively isolated feces, suggesting that latrines belonged to the most frugivorous mammal species or individuals.

Association in seed numbers of plant species pairs

In the *Pistacia*-dominated shrubland, bivariate mark correlation function indicated that seed numbers of *Pyrus–Chamaerops* pair were significantly (Fig. 4A; rank = 200, $P = 0.005$) aggregated at small spatial scales (up to 60 m; i.e., intra-latrine aggregation). For *Pyrus–Pistacia* (Fig. 4B) and *Chamaerops–Pistacia* (Fig. 4C), we found significant (rank $\geq$197, $P \leq 0.05$) aggregation at large spatial scales (~400 m) neighbored by slight negative departures. This is probably related to the existence of a few large clusters located at similar distances and comprising many feces, mostly from badgers (i.e., inter-latrine aggregation; Fig. 1A).

In the *Juniperus*-dominated shrubland, for *Corema–Juniperus* and *Corema–Rubus* pairs, we found no significant (rank $\leq$52, $P \geq 0.745$) seed aggregation at any spatial scale (Fig. 4D, E). For the pair *Juniperus–Rubus*, there was a slight but significant (rank = 195, $P = 0.030$) aggregation at small spatial scales (20–30 m; i.e., intra-latrine aggregation; Fig. 4F).

Because most recovered seeds in the *Halimium*-dominated shrubland belonged to *R. ulmifolius*, in this case we pooled seeds of species other than *R. ulmifolius* (*Pyrus*, *Chamaerops*, and so forth) into a single category called "Other spp." The observed bivariate mark correlation function indicated no significant (rank = 47, $P = 0.770$) aggregation for *Rubus* and the pool of all other fleshy-fruited species at any spatial scale (Fig. 4G). Overall, these results indicated that, once the strong aggregation of fecal samples in the three study sites was controlled for, there were significant positive associations in seed numbers for some pairs of fleshy-fruited species, with this mechanism of seed aggregation being most marked in the *Pistacia*-dominated shrubland.

DISCUSSION

Diverse mechanisms are likely to generate spatial contagion of dispersed seeds because nearly any disperser species interacts with a variety of plant species, and different species of dispersers mediate dispersal of any given plant species (e.g., Carlo et al. 2003, Nathan 2007, Fedriani et al. 2010, Côrtes and Uriarte 2013). However, detailed characterizations of such complex seed rains have been curtailed both because the appropriate analytical tools have not been fully avail-

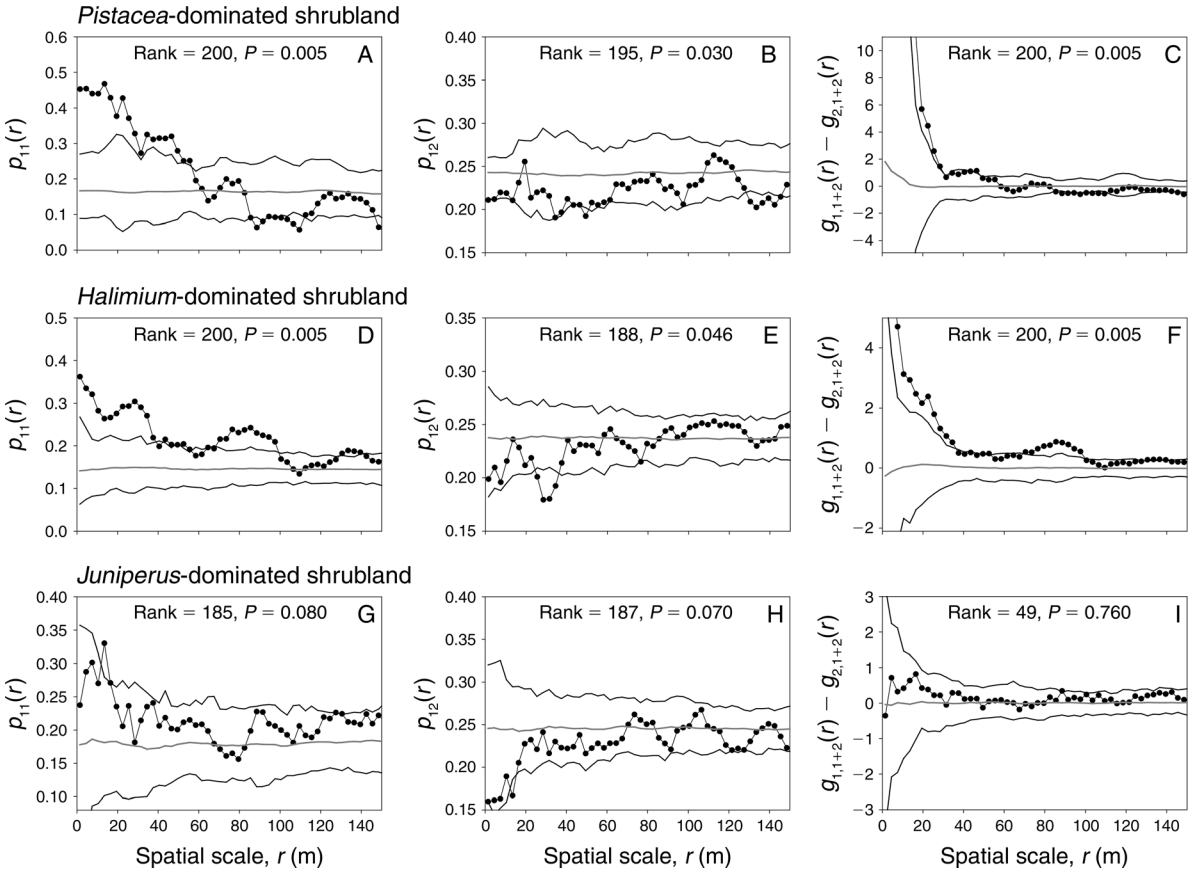

FIG. 3. Analysis of feces with seeds in the three studied shrublands using mark connection functions as summary statistics. (A, D, G) The mark connection function $p_{11}(r)$ gives the conditional probability that, from two mammal feces that are separated by distance r, both are type 1 (i.e., with seeds). (B, E, H) The mark connection function $p_{12}(r)$ gives the conditional probability that, from two mammal feces that are separated by distance r, the first is type 1 (i.e., with seeds) and the second is type 2 (i.e., without seeds). (C, F, I) The test statistic $g_{1,1+2}(r) - g_{2,1+2}(r)$ compares the density of feces (i.e., $1 + 2$) around feces with seeds (i.e., type 1) with the density of feces (i.e., $1 + 2$) around feces without seeds (i.e., type 2). The expected value of the test statistics is zero under random labeling, but if feces containing seeds would occur more frequently in clusters of feces (latrines), we would expect $g_{1,1+2} > g_{2,1+2}$. The expected mark connection function statistics (gray solid line) and the corresponding simulation envelopes (black solid lines; the 5th lowest and highest values of the mark connection functions created by 199 simulations under random labeling) are also shown.

able until recently and because of the technical difficulty of linking individual species of frugivores to individual disseminated seeds. We showed that spatial point pattern analysis can be used to successfully characterize compound multispecies seed rains and to identify the proximate mechanisms of seed aggregation in complex seed-disperser networks. Moreover, our approach does not require the identification of seed-disperser species, an advantage that make it applicable in a myriad of systems and logistic circumstances.

We revealed nonrandom spatial structures at the three target organizational scales of observed seed rains: all feces, feces with seeds, and the interspecific relationships of seed species pairs. Our results thereby exposed, for the first time, three proximate mechanisms by which seeds of different fleshy-fruited shrub species aggregate across a range of spatial scales. First, as found in previous studies (e.g., Schupp et al. 2002, Russo and Augspurger 2004, Westcott et al. 2005), the three local guilds of frugivore mammals tended to deliver their feces in an aggregated fashion, with an overall pattern of fecal delivery that could be described well by a nested double-cluster Thomas process in all three independent study sites. Second, once the strong observed fecal aggregation was accounted for, the distribution of feces with seeds was clustered within the pattern of all feces (i.e., with and without seeds) and the density of fecal samples including seeds was higher than expected around other feces comprising seeds in both the *Pistacia*- and *Halimium*-dominated shrublands. This intriguing pattern reveals an overlooked mechanism of mono- and multispecific seed aggregation for endozoochores acting in synergy with other mechanisms of seed aggregation and thus enhancing the likelihood of interspecific seed interactions (e.g., Veech 2000, Enders and Vander Wall 2012, Ostoja et al. 2013). Finally, mark correlation analyses

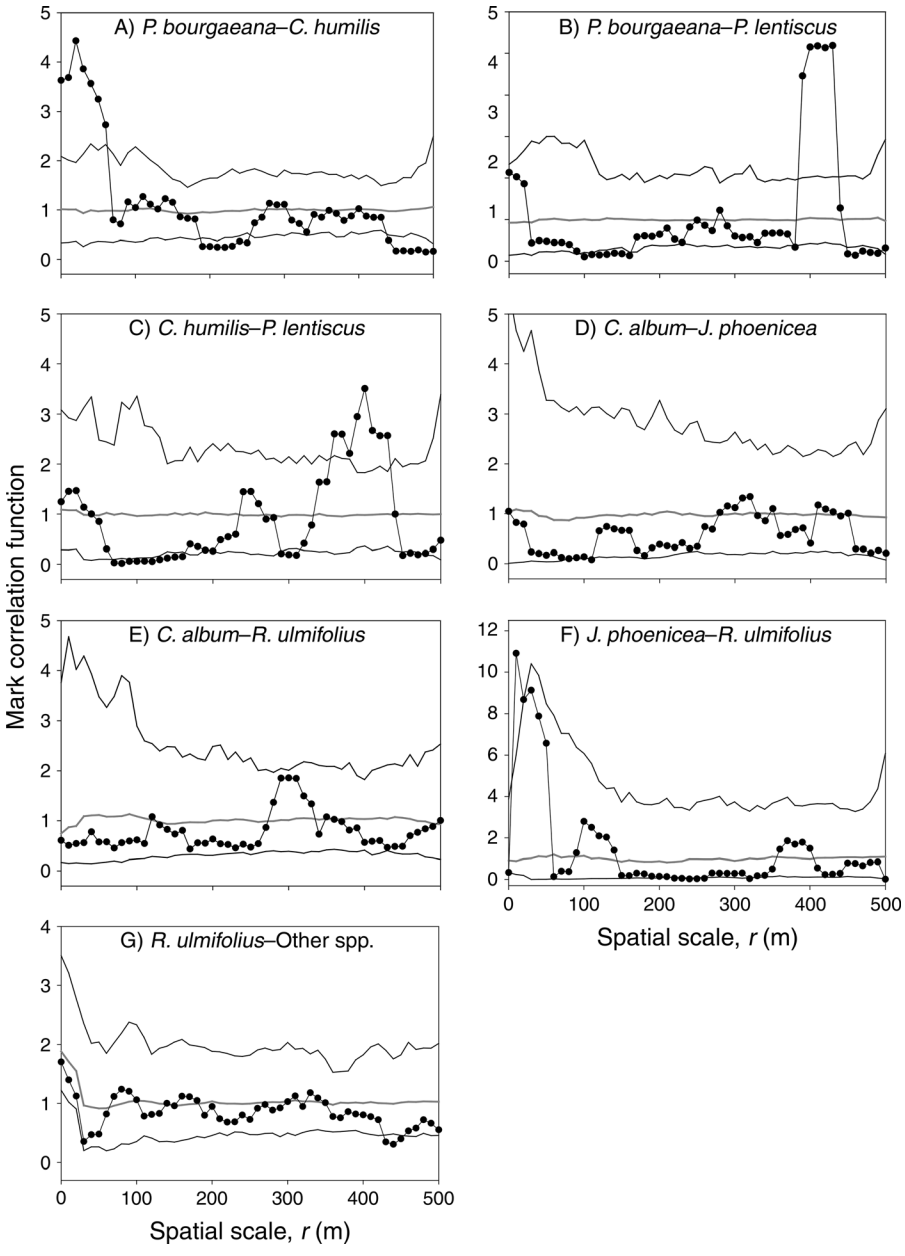

FIG. 4. Bivariate mark correlation functions used to quantify potential spatial interspecific associations in the number of seeds in mammal feces. To test if the observed mark correlation function indicates nonrandom spatial correlations in the number of seeds of two species (m_1, m_2), we contrasted it to a null model that shuffled the mark pairs (m_1, m_2) attached to the given feces together over all feces. The expected mark correlation function (gray solid line) and the corresponding simulation envelopes (black solid lines depicting the 5th lowest and highest values of the mark correlation functions created by 199 simulations under random labeling) are also shown.

revealed a third neglected seed aggregation mechanism by which the numbers of seeds in feces tended to be positively associated at distinct spatial scales for several shrub species pairs. For example, whereas seeds of *Pyrus–Chamaerops* and *Juniperus–Rubus* were positively associated at small spatial scales (i.e., $\leq$10 m), seeds of *Pyrus–Pistacia* and *Chamaerops–Pistacia* were positively associated at larger scales (i.e., ~400 m). These positive associations may be related to different ultimate causes, such as selection by individual frugivores of complementary fruit species (Whelan et al. 1998), or the formation through the dispersal season of multispecific seed aggregates (Kwit et al. 2004, 2007; J. M. Fedriani and T. Wiegand, *unpublished data*). Moreover, our results highlight the need for multi-scale approaches to comprehensively assess the seed rain patterns generated

by diverse communities of seed dispersers. Although spatially contagious seed dispersal has been documented previously (Schupp et al. 2002, Russo and Augspurger 2004, Westcott et al. 2005), our results are pioneering in revealing that seed aggregation can emerge from different disperser behaviors and mechanisms acting at different spatial scales and, thus, with potentially different outcomes for propagule success.

Even though clustering at different spatial scales has been predicted for seed rains generated by different seed dispersers (Howe 1989, Russo and Augspurger 2004, Wiegand et al. 2009), it seldom has been demonstrated. In our target Mediterranean shrublands, badgers are known to create large latrines with strong aggregation at small scales; deer and red foxes deliver feces in a relatively scattered fashion; and wild boars show an intermediate pattern of fecal aggregation (Lloyd 1980, Kruuk 1989, Fedriani et al. 2010). Adding together such varied fecal marking behaviors produced a compound patterning of seed aggregation that did not correspond to either the strong aggregation typical of badgers or the scattered spatial pattern typical of deer and fox. Importantly, it is precisely such compound patterning that is "perceived" by plants. Therefore, robust analytical approaches such as the one presented here should be adopted to characterize contagious seed dispersal of complex seed-disperser networks.

The comparison of results from our three study sites suggests that the more badger activity in a particular area, the stronger the seed aggregation, probably because it was the species showing the most aggregated fecal marking behavior (Kruuk 1989, Fedriani et al. 2010). For example, in the two areas with high badger activity (the *Pistacia*- and *Halimium*-dominated shrublands), the neighborhood density at small scales was several times higher than in the *Juniperus*-dominated shrubland, where badger activity was low. Also, in the two areas with higher badger activity, feces containing seeds were strongly aggregated at small spatial scales (Fig. 3A, D) and were usually associated with large fecal clusters (i.e., latrines; Fig. 3C, F), whereas in the *Juniperus*-dominated shrubland, such trends were much weaker (Fig. 3G, I). Overall, these results strongly suggest that a single disperser species can have a major influence on the compound seed rain generated by a guild of dispersers, an idea that deserves further research.

The first identified mechanism of seed aggregation is related to mammal fecal marking behavior (e.g., Fragoso et al. 2003, Russo and Augspurger 2004), which rendered a compound pattern of fecal delivery that followed a nested double-cluster Thomas process. The Thomas process has some particular assumptions, most important being that feces are randomly distributed over the clusters. Except for badgers at the *Pistacia*-dominated shrubland (which showed extreme levels of clustering difficult to describe), we found that the assumption of a random number of feces within clusters was reasonably met. This was revealed by the test of the fitted cluster processes with the distribution function of the distances to the nearest neighbor, which is particular sensitive to this (Wiegand et al. 2007, 2009), and the spherical contact distribution, which tested the distribution of gaps in the pattern (note that the pair correlation function cannot reveal this; Figs. 1 and 2). The alternative would be that some clusters contained more seeds than expected by the random assignation of the Thomas processes and other less, which would lead to a high proportion of "isolated" feces. Thus, although feces were certainly very clustered, the observed pattern followed the simplest and "most random" clustering in which the number of feces per cluster approximated a Poisson distribution. This is an interesting result that indicates no sophisticated method of fecal aggregation over the clusters; thus, besides being aggregated, fecal delivery followed the most random model. Therefore, our approach can be used in other seed-disperser networks to identify this first mechanism of contagious seed dispersal generated by different dispersers and to test ad hoc the level of agreement between the observed and predicted aggregation functions.

The level of seed aggregation has been proposed as an important aspect of the qualitative component of seed dispersal effectiveness at the community level (sensu Schupp et al. 2010) that can be effectively examined by means of both random labeling and mark correlation function analyses. Such seed aggregation can have far-reaching consequences for plant recruitment. For instance, when seeds are strongly clustered at small scales, chemical exudations from germinating seeds are likely to accelerate, delay, or even impede germination by conspecific or multispecific seeds (Loiselle 1990, Murray 1998). Moreover, clustering of dispersed seeds can alter the likelihoods of predation for individual seed species as a result of high overall density and/or the relative proportions of different seed species (e.g., Emerson et al. 2012, Ostoja et al. 2013). Some species occurring in multispecies seed aggregations may confer "associational resistance" (sensu Tahvanainen and Root 1972) to seed predators of other seed species, whereas in other cases, the presence of a species might increase the susceptibility of other seed species to predation (i.e., "associational susceptibility"; Barbosa et al. 2009, Ostoja et al. 2013). Furthermore, given that contagious seed rains tend to give rise to aggregation of subsequent plant ontogenic stages (e.g., seedlings, saplings; Wang and Smith 2002), similar processes can arise also beyond the seed stage. For example, associational effects altering the susceptibility to herbivory of individual seedling species as a result of the presence of a second species have been documented (Callaway 2007). Contagious seed dispersal may therefore profoundly affect the structure and dynamics of plant communities. Consequently, rigorous analyses of spatial contagion of dispersed seeds at varying scales can help to predict a number of plant–plant and plant–animal post-dispersal

interactions and, thus, to forecast the dynamics of plant populations and communities.

We revealed for the first time how contagious seed dispersal in complex seed-disperser networks can arise by means of complementary proximate mechanisms acting synergistically at a range of spatial scales, and we provided a robust approach that can be applied widely to many other seed-dispersal systems (for reviews, see Schupp et al. 2002, Kwit et al. 2007). For instance, mapped multispecific seed rains generated by rodents (e.g., Beck and Vander Wall 2010), ants (e.g., Fedriani et al. 2004), and diverse diplochorous systems (sensu Vander Wall and Longland 2004) are likely to benefit from our approach. Further research is needed on the population and community consequences of contagious seed dispersal, and to assess the consistency of patterns reported here (e.g., nested double-cluster Thomas process, the importance of single disperser species on overall seed rains) over a broader range of systems. Despite the relative invariant patterning of seed clustering, our study also shows that some attributes of endozoochore seed rains (e.g., intensity, scales of aggregation) are likely to be variable in space and time as a consequence of changes in the ecological context (Agrawal et al. 2007) in which seeds and their dispersers interact.

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